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ORIGINAL ARTICLE

Cascading Effects of Apex Predator Recovery on Rodent Foraging Activity and Seed Predation

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Abstract

Apex predators can trigger trophic cascades that shape plant–animal interactions. By suppressing medium-sized carnivores, apex predators may indirectly influence small prey behavior and abundance, altering key ecosystem functions such as post-dispersal seed predation. We investigated cascading effects of the Iberian lynx (*Lynx pardinus*) on rodent foraging activity and predation of *Pyrus bourgaeana* seeds in southern Spain, comparing sites with lynx presence and absence (low vs. high mesopredator abundance, respectively). We deployed 1152 seeds at 144 seed depots and used 36 camera traps to monitor rodent activity and foraging. We analyzed how predation risk, habitat, and microhabitat influenced (1) seed predation, (2) seed encounter probability, (3) number of visits to seed depots, and (4) visit duration. Seed predation rates were unaffected by lynx presence (57% vs. 43%), but this apex predator altered multiple aspects of rodent foraging activity. Seed encounter probability was 88% greater with lynx absent. In lynx presence, non-consumptive visits in forest habitats were 83% greater and visit duration rose 59-fold compared to lynx absence. The number of visits to seed depots was 85% greater with lynx present, but shrub microhabitats received more visits with lynx absent. Rodent abundance positively affected the number of visits and seed predation but did not vary with lynx presence. These behavioral changes in post-dispersal seed predation may ultimately affect seed dispersal success and thereby plant recruitment. Our findings underscore the role of apex predators in modulating ecosystem functions via non-lethal pathways and the importance of behaviorally mediated trophic cascades for plant–animal interactions.

Graphical Abstract

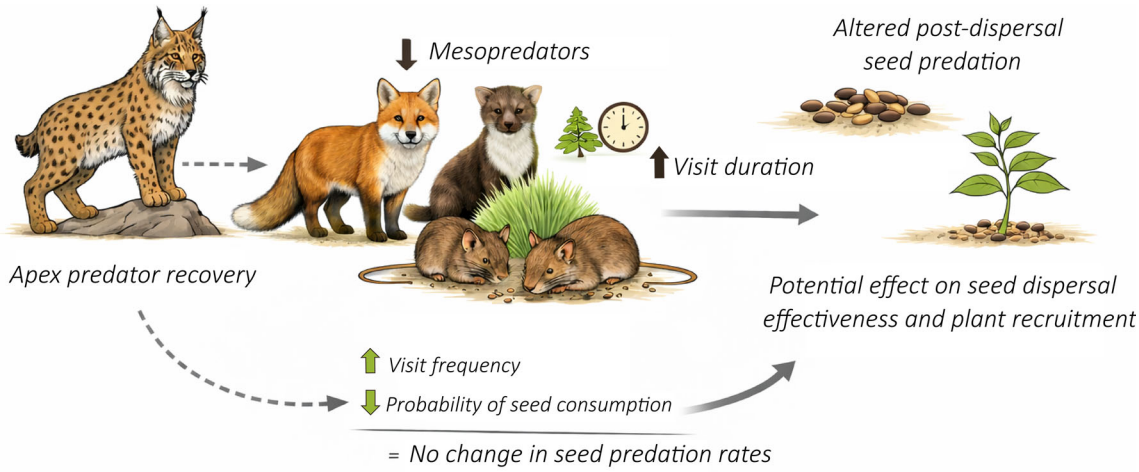
The recovery of the Iberian lynx (Lynx pardinus) triggers a behaviorally mediated trophic cascade by modifying the foraging behavior of seed-eating rodents, with potential consequences for post-dispersal seed dynamics and plant recruitment

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Highlights

- Apex predators can indirectly shape rodent foraging and seed predation patterns.
- Behavioral plasticity keeps stable seed predation rates across predation risk scenarios.
- Rewilding efforts should link predators and trophic cascades to ecosystem services.

Key words: behaviorally mediated trophic cascade; food web; granivorous rodents; iberian lynx; mammal carnivores; mesopredator release; predation risk..

Introduction

Apex predators have experienced significant population declines and range contractions over the past centuries due to habitat loss and fragmentation, overexploitation, and direct persecution by humans (Ritchie and Johnson 2009; Ripple and others 2014a). These species occupy the top of trophic chains and play a crucial role in preserving global biodiversity (Duffy 2003; Sergio and others 2008; Terborgh and others 2010). Therefore, maintaining or recovering predator populations within an ecologically functional density range is a key objective for sustaining ecosystem structure and function (Ritchie and others 2012; Ripple and others 2014a). However, the ecological effects of apex predators extend beyond direct predation. Apex predators can trigger cascading effects that reshape the behavior, distribution, and ecological roles of prey and subordinate predators (Estes et and others 2011; Suraci and others 2016; Burgos and others 2023). Thus, understanding how these top-down forces operate is essential to predict ecosystem responses to apex predator rewilding.

Apex predators exert top-down control on ecosystems in part by suppressing mesopredators, through both direct killing and behavioral interference (Ritchie and Johnson 2009; Letnic and others 2012; Burgos and others 2023). This intraguild suppression can prevent ''mesopredator release,'' a phenomenon where the absence of apex predators leads to mesopredator proliferation and increased predation pressure on smaller prey (Courchamp and others 1999; Crooks and Soulé 1999; Brook and others 2012). Such dynamics can affect prey population sizes, spatial distribution, activity patterns, and foraging behavior (Ordiz and others 2013). While the reintroduction or recovery of apex predators could positively impact ecosystems and indirectly benefit other species (Sergio and others 2008; Letnic and others 2012; Ripple and others 2014b; Burgos and others 2024), it may also generate unexpected or context-dependent outcomes for ecosystem functioning depending on the functional roles of both predators and prey.

Although it is well known that the recovery of apex predators can lead to controlling populations of large prey such as herbivores (Ripple and Beschta 2012), few studies have addressed the cascading effects on prey shared with mesopredators, such as small mammals (but see Norrdahl and Korpimäki 1995; Moseby, Hill and Read 2009; Letnic, Ritchie and Dickman 2012; Burgos and others 2023). In this context, Miller and others (2012) demonstrated that, in a scenario of wolf reintroduction, the abundance of rodents increased

around wolf dens, likely due to a general reduction in predation pressure as a result of mesopredator control. Small mammals are prey for many medium-sized carnivores (Carvalho and Gomes 2004) and have evolved anti-predatory behaviors, often involving changes in their activity patterns and habitat use—such as reducing foraging effort in risky areas or shifting toward habitats that provide greater cover (Brown and others 1988; Díaz and others 2005; Navarro-Castilla and Barja 2014).

Given that small mammals play vital roles in ecosystem functioning, such as seed dispersal and predation (Fedriani and Delibes 2013; Galetti and others 2015a; Godó and others 2022), the recovery of large carnivores could also impact these functions. Rodent population increases may intensify seed predation in ecosystems devoid of mesopredators (Meserve and others 2003; Garrote and others 2019). Seed predators can reshape the initial seed rain by modifying the density and spatial distribution of seeds, and ultimately affecting plant recruitment (García and others 2005; Calviño-Cancela 2007; Pías and others 2014). For example, de Paula and others (2018) showed that the loss of large mammals (tapirs *Tapirus spp.* and large cats, family *Felidae*) reduced seed dispersal while increasing seed predation, triggering cascading effects on forest biomass and tree diversity. Moreover, anti-predatory behaviors in seed predators may lead to behaviorally mediated trophic cascades that alter seed predation patterns and seedling establishment. However, few studies have explored how shifts in predator–prey communities affect seed predation and subsequent plant recruitment (Gutiérrez and others 1997; Maron and others 2010; Pender and others 2013; Bartel and Orrock 2021; Morán-López and others 2022).

The seed-arrival site can play a crucial role in mitigating seed predation, particularly when certain seed predators reach high abundances (Hulme 1994; Garrote and others 2019; Bartel and Orrock 2021). Conflicts between seeds and seedlings may also arise during plant establishment, as local conditions can favor seed survival while hindering recruitment (Schupp 1995; Burgos and others 2025). For instance, dispersal beneath nurse plants often enhances seedling survival (Gómez-Aparicio and others 2004; Garrote and others 2021). However, vegetation cover may reduce perceived predation risk for small mammals (Rosalino and others 2011; Loggins and others 2019), potentially increasing seed predation in more covered sites (Rey and others 2002; Sanguinetti and Kitzberger 2010). Thus, monitoring the foraging habitat preferences of seed predators is critical to understanding the environmental factors that influence post-dispersal processes (Izhaki and others 1991; Calviño-Cancela 2007; Donoso and others 2016; García-Cervigón and others 2018). This becomes especially relevant in predator reintroduction scenarios, where behavioral responses of seed predators to predation risk may shape plant colonization trajectories and thus inform long-term conservation planning.

In this study, we experimentally assessed the potential effects of reintroducing an apex predator, the Iberian lynx (*Lynx pardinus*), on the foraging behavior and seed predation rates of rodents in southern Spain. Given that rodents are key prey for mesopredators, we hypothesized that lynx presence would trigger a trophic cascade by reducing mesopredator abundance (Burgos and others 2023), thereby increasing rodent populations and seed predation rates. We also expected that, in the presence of lynx, rodents will exhibit higher foraging activity due to a lower perceived risk, which would further contribute to increased seed predation rates. However, we expected that the type of habitat and the microhabitat will modulate the foraging activity and seed predation rates of rodents. Vegetation cover would provide rodents with safe spaces (that is, low perceived risk of predation), thereby resulting in higher seed predation rates and foraging activity, especially in lynx absence (that is, high mesopredator abundance).

Methodology

Study Area

The study was conducted in the Sierra de Andújar Natural Park (SANP), located in Sierra Morena in southern Spain (38°14′27.71′′ N, 4° 4′45.03′′ W, approximately 740 km^2). The elevation ranges from 400 to 800 m above sea level. The region experiences a mild average annual temperature (~ 18 °C) and low precipitation (~ 700 mm), typical of Mediterranean climate zones (AEMET Opendata 2020). The SANP is characterized by extensive large-game hunting estates. Although occasional fox culling may be authorized in some estates—since this is a game species—no predator control or poaching activities had been carried out recently in the specific properties where our study took place. The dominant vegetation in the SANP is Mediterranean shrubland, but two main habitat types characterize the landscape (Figure 1). The predominant is mature forest with high tree cover, dominated by holm oak (*Quercus ilex*), and accompanied by a diverse community of fruit-bearing

shrubs such as strawberry tree (*Arbutus unedo*) and aromatic species like rosemary (*Rosmarinus officinalis*). The second is open landscape, composed of grasslands interspersed with scattered shrubs and trees, including species like the Iberian pear (*Pyrus bourgaeana*), which is especially common in these open areas (Figure 1).

The SANP is home to one of the largest wild Iberian lynx populations that has recovered from near-extinction in the 1990s without the need for reintroductions. Thanks to successive conservation efforts—such as habitat management and the recovery of key prey like wild rabbits (*Oryctolagus cuniculus*)—the current SANP population exceeds 250 individuals (MITECO 2023). However, the lynx' distribution remains heterogeneous throughout the SANP (see Burgos and others 2023). The lynx coexists with a rich community of mesopredators in the SANP, including the red fox (*Vulpes vulpes*) and the stone marten (*Martes foina*). This feline typically regulates the abundance of these mesopredators (Jiménez and others 2019) and can alter their foraging behavior, habitat use, and therefore, their seed dispersal patterns (Burgos and others 2023, 2024, 2025). The most common small mammals that are regular prey of the mesopredators in the SANP include the wild rabbit and rodents such as the garden dormouse (*Eliomys quercinus*), the wood mouse (*Apodemus sylvaticus*), and the Algerian mouse (*Mus spretus*). These small mammals consume the pulp and seeds of various fruit-bearing plant species (Rey and others 2002; Fedriani and Delibes 2013). In lynx rewilding scenarios, the

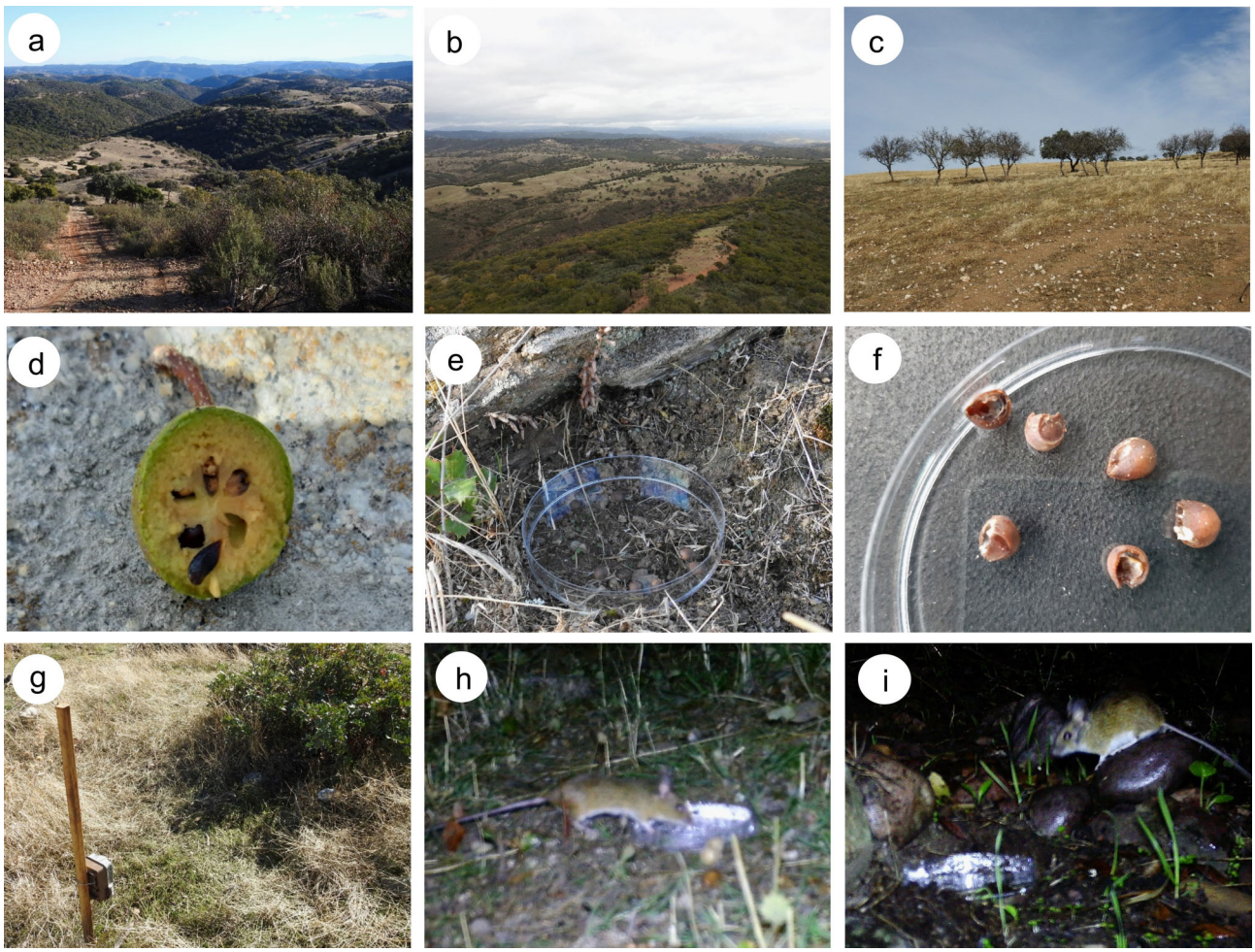


Figure 1. (a–c) Photographs illustrating the landscape structure in the SANP and the habitat types selected for this study (open vs. forested). (d) Example of manual seed extraction from *P. bourgaeana* fruits. (e) Placement of seeds in a Petri dish for the seed predation experiment. (f) *P. bourgaeana* seeds predated by rodents in our seed predation experiment. (g) Example of camera-trap installation for the seed predation experiment. (h–i) Images of a wood mouse (*A. sylvaticus*) captured by camera traps set up for the seed predation experiment.

abundance of small mammals increases due to a decrease in overall predation pressure (Burgos and others 2023).

Experimental Design

We compared the relative abundance and foraging activity of rodents, as well as seed predation rates, at two locations within the SANP: one with Iberian lynx presence (one year-round territorial couple) and a control location without lynx. Presence and absence of lynx were estimated by a previous camera-trapping study (120 camera traps; 10,644 trap-days) in the same area (Burgos and others 2023), which provides a highly reliable detection method for this species. These data were further corroborated by scat surveys (Burgos and others 2024) and personal information from the Iberian lynx monitoring project who have long monitored lynx individuals through GPS collars. Given that seed removal, and rodent abundance and activity can vary significantly among habitats and microhabitats (for example, Hulme 1994), we also accounted for these factors in our experimental design. At each study location, we selected two different habitat types: a) mature forest with a dense shrub stratum and b) open landscapes with sparse shrub vegetation and small clusters of isolated trees (Figure 1). Within each habitat type, we identified three microhabitats: a) under a rock (referred to as rock), b) under a shrub (referred to as shrub), and c) in an open area with no vegetation cover (referred to as open). These microhabitats were the most selected by frugivorous mesopredators to deposit their feces, and therefore, the ingested seeds, in a previous study in the same area (Burgos and others 2025).

Seed Predation Experiment

To assess the effect of Iberian lynx presence on rodent seed predation rates, we conducted a seed predation experiment using *P. bourgaeana* as the study species. Seed predation data have been already published in a previous study as part of a SEM model aimed at evaluating the net effect of Iberian lynx presence across the full life cycle of *Pyrus bourgaeana*, from seed dispersal to seedling recruitment (Burgos and others 2025). This Mediterranean tree produces large-sized fruits (2–3 cm in diameter and ~ 9.5 g) whose seeds are frequently consumed by rodents (Fedriani and Delibes 2009a; Suárez-Esteban and others 2018; Garrote and others 2019). Each tree produces between 100 and over 1000 fruits, with each fruit containing 1–5 viable seeds. The selected microhabitats are common sites where the main dispersers of *P. bourgaeana* (for example, foxes and badgers; *Meles meles*) deposit seeds, making them available for seed predators (Fedriani and Delibes 2009b; Fedriani and others 2010; Burgos and others 2025).

The seed predation experiment was conducted in November 2020, coinciding with the peak of *P. bourgaeana* fruiting and seed dispersal (Fedriani and Delibes 2009a). We used seeds extracted from wild fruits collected 1-week before the experiment. Seeds were directly placed on Petri dishes (see Figure 1) in each study location, habitat type (forest and open), and microhabitat (rock, shrub, and open), simulating naturally dispersed seeds. In each habitat type, we set up seed depots in six plots (15 × 15 m, spaced 200 m apart) which can be considered spatially independent given the small territory size of rodents in Mediterranean ecosystems (~ 1 ha, Muñoz and others 2009; Rosalino and others 2011). In each sampling plot, we selected shrubs (~ 1 m in height) and rocks (~ 0.5 m in height) of similar size for the seed depots. The most common shrub species selected were *Pistacia lentiscus* and *Rosmarinus officinalis*. Each microhabitat was replicated twice within each 15 × 15 m plot. We visually estimated the percentage of shrub, tree, and rock cover within a 15 m radius from the center of each plot, as these structural elements can influence rodent foraging behavior and potentially affect seed removal rates. Forest habitats showed greater shrub (mean ± 1SE = 35.7 ± 1.3 vs. 4.8 ± 0.6) and rock cover (24.0 ± 0.7 vs. 10.8 ± 0.3) compared to open habitats ($P < 0.001$ for both). Across lynx scenarios, only shrub cover differed significantly, being higher on average in areas without lynx (no lynx: 30.9 ± 2.2 vs. lynx: 13.6 ± 1.1; $P < 0.001$).

We placed eight seeds per Petri dish on the first day of the experiment, monitored them for five consecutive days, and recorded the daily accumulated number of seeds consumed. A total of 1152 seeds were dispensed (8 seeds per dish × 2 replicates × 3 microhabitats × 6 plots × 2 habitats × 2 lynx scenarios). Sampling was conducted on nights without a full moon to avoid reduced rodent activity under moonlight (Navarro-Castilla and Barja 2014). We assumed that seed removal corresponded to seed predation, as seed predation by rodents was confirmed by camera traps (see below), and we often observed seed shells consumed by rodents (Garrote and others 2019; Figure 1). Seed predation rates (proportion of seeds removed) per depot in each location, habitat, and microhabitat were calculated as the total number of seeds

predated after five days divided by the total number of seeds dispensed. Camera-trap footage confirmed that seed removal events were attributable to rodent predation in 92% of seed depots. All mismatches corresponded to cases where visual checks confirmed seed predation by rodents but the cameras failed to record it, likely due to sensor failure or undetected nocturnal visits.

Estimation of Rodent Foraging Activity Patterns

To assess rodent foraging activity patterns, we installed 36 camera traps (Scoutguard SG562-C; white LED) at a subset (25%) of the seed depots. We placed 18 cameras in each lynx scenario: nine in forest habitats and nine in open habitats, with three cameras in each type of microhabitat. The cameras were positioned at a height of 20–60 cm above the ground, mounted on wooden stakes or available logs, 1–2 m from the seed depot (see Figure 1). They operated continuously (24 h) throughout the 5-day seed predation experiment. The cameras were set with a 1-s trigger delay to capture three consecutive images, with high sensitivity. For each rodent visit captured by the cameras, we recorded the time of day (UTC), the duration of each visit (the time in seconds from the first to the last photo), and the seed encounter probability. We defined a seed encounter (coded as 1) as any case in which the rodent manipulated the seed and was visibly observed consuming it. Since *Pyrus bourgaeana* seeds are relatively large ($\sim$ 1 cm), rodents typically predate them by gnawing the coat and consuming the inner contents rather than ingesting them whole, often leaving behind pieces of empty seed coats (see Figure 1f). Visits were considered independent if there was a gap of more than 5 min between consecutive photos. While there is no standardized threshold for defining independent behavioral events, this interval has recently been proposed as a practical and conservative criterion in camera-trap protocols for animal behavior studies (Villalva and Jordano 2025). We calculated the number of visits to seed depots as the total number of independent visits per camera trap.

To estimate the abundance of rodents in our study sites, we conducted livetrapping using Sherman traps (model LFA; 7.6 × 8.9 × 22.9 cm) one week after completing the seed predation experiment. We placed five traps in each of the six plots where the seed predation experiment was conducted, specifically under shrubs, as this microhabitat is most suitable for rodent capture and provides thermal insulation (Torre and Díaz 2004). In total, 120 Sherman traps were dispensed (5 traps per plot × 6 plots × 2 habitats × 2 lynx scenarios) over three consecutive nights. The traps were set up during the day and baited with a piece of sardine to attract rodents. Hydrophobic cotton was also placed inside the traps as bedding material to prevent hypothermia during cold nights, while also serving as a dry, nest-like shelter for animal welfare (Torre and others 2023). Traps were checked early each morning to record the captured species and release the animals immediately. As our aim was to estimate relative abundance rather than absolute density, and to minimize handling stress, we did not apply individual marking techniques. The rodent relative abundance index (RAI) was calculated as the total number of captures and recaptures divided by the number of active traps per night for each lynx scenario and habitat type.

Statistical Analyses

To evaluate the effects of Iberian lynx presence on rodent seed predation patterns and foraging activity in our seed predation experiment, we fitted generalized linear mixed models (GLMMs) and generalized linear models (GLMs) using the R package lme4 version 1.1–27.1 (Bates and others 2020).

We analyzed the following response variables: (1) seed predation rates (including zero), (2) seed encounter probability (Bernoulli distribution: 0, 1), (3) number of visits to seed depots (including zero), and (4) visit duration. We used binomial errors for the seed predation rates and the seed encounter probability, Poisson errors (log link) for the number of visits and Gaussian for the visit duration. Seed predation rates were derived from visual inspections of the seed depots, whereas the remaining variables were obtained from camera-trap data.

We used the presence or absence of the Iberian lynx (L) as a fixed factor in all models. Habitat type (H: forest vs. open) and microhabitat type (M: shrub, rock, open) were included as fixed factors in the models for seed predation, number of visits, and visit duration. We excluded habitat and microhabitat for the seed encounter probability due to overfitting. Interactions between L x H and L x M were included in their respective models to account for differential effects between lynx scenarios (presence vs. absence). The interaction H x M was also included. Canopy cover (T), shrub cover (S), and rock cover (R), measured at the sampling plot level, were included as covariates in all models. The relative abundance index of rodents (RAI) was included as a covariate in the seed predation, number

of visits and visit duration models. For the seed predation and number of visits, the number of days the experiment was active was included as an offset. The sampling plot (n = 24) was included as a random effect in the seed predation model, and the camera (n = 36) was included as a random effect in the visit duration model. In the remaining models, random effects were not included as model selection based on the corrected Akaike Information Criterion (AICc) indicated that mixed and non-mixed models were equivalent ($\Delta AICc \leq 2$).

Model Selection

The proposed models included all fixed effects and interaction terms described above. We selected candidate models based on their AICc values. If no other model was within two AICc units of the top-ranked model ($\Delta AICc = 0$), the top model was considered the best; however, if other models were within two AICc units of the top model ($\Delta AICc \leq 2$), these were considered a set of models with similar support (Burnham and Anderson 2002). Model selection was conducted using the MuMIn package v.1.43.17 (Barton 2013). We calculated marginal and conditional R^2 coefficients (pseudo-R^2) for the selected models (Nakagawa and others 2017). Post hoc pairwise comparisons were performed to estimate model coefficients for interaction terms and factors using the R package emmeans v.1.6.3 (Russell V. and others 2021). Model residuals were inspected using the DHARMa package v.0.4.6 (Hartig and Lohse 2022). All analyses were conducted in R (version 3.6.1; R Core Team 2019).

Results

Overall Patterns

We livetrapped a total of 32 rodents from three different species: *A. sylvaticus* (n = 29), *M. spretus* (n = 2), and *E. quercinus* (n = 1). The relative abundance of rodents (RAI) in lynx presence (Mean ± SE = 13.3 ± 3.6) was higher than in lynx absence (9.2 ± 3.6), such differences were not significant ($Chi^2 = 0.61$, d.f. = 1; P = 0.43). Camera traps confirmed that rodents were the sole seed predators in our experiment (see Figure 1), with *A. sylvaticus* dominating detections (> 80%), a single

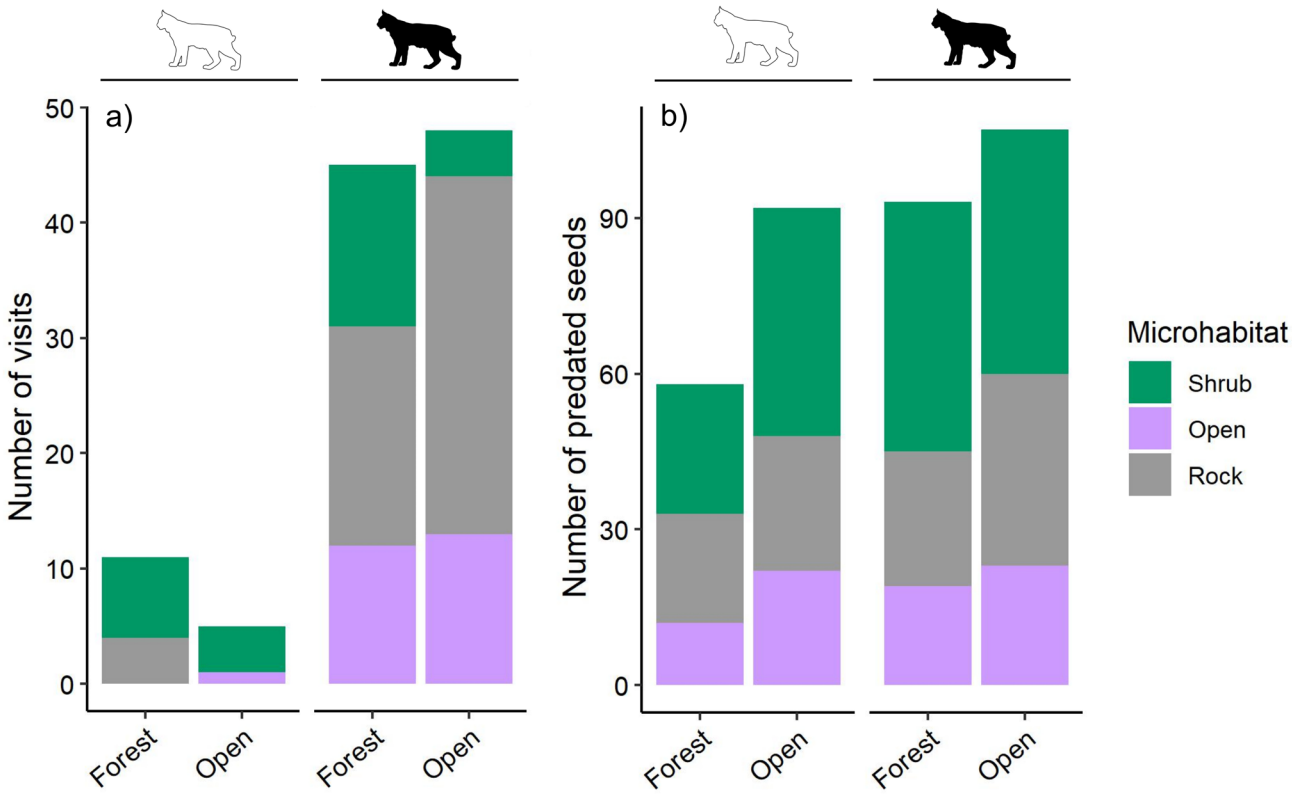


Figure 2. (a) Total number of visits recorded during the seed predation experiment and (b) total number of seeds predated according to habitat type (forest vs. open), microhabitat type (shrub, rock, and open), and lynx presence scenario. Lynx absence is represented by white-lynx silhouette and lynx presence by black-lynx silhouette.

Table 1. Models within 2 ΔAICc Built to Explain the Foraging Behavior and the Seed Predation Patterns of Rodents Through the Following Response Variables: 1) Seed Predation Rates (Proportion of Seeds Removed Obtained Through Visual Checks), 2) Seed Encounter Probability (Probability of Seed Consumption, 0–1, Based on Camera-trap Footage), and 3) Number of Visits to Seed Depots (Based on Camera-trap Footage)

Response	L	SP	H	M	RAI	S	R	T	LxH	LxM	HxM	K	Loglik	AICc	ΔAICc	W	R^2_c	R^2_m
(1) Seed predation rate	-		-	X***	X***	-	-	-	-	-	-	5	-331.10	672.63	0	0.15	0.92	0.46
	-		-	X***	X***	X	-	-	-	-	-	6	-330.84	674.30	1.67	0.07	0.92	0.47
	-		-	X***	X***	-	-	X	-	-	-	6	-330.96	674.54	1.91	0.06	0.92	0.47
(2) Seed encounter probability	X**					X*	-	X*				4	-47.38	103.14	0	0.54	-	0.14
(3) Number of visits	X		X**	X	X***	X***	X*	-	X	X***	-	11	-56.69	146.37	0	0.43	-	0.83
	X		-	X	X***	X**	X***	-	-	X**	-	9	-61.48	147.89	1.51	0.20	-	0.82

L: lynx (presence vs. absence), SP: seed encounter probability (0, 1), H: habitat (forest vs. open), M: microhabitat (rock, shrub, open), RAI: relative abundance index of rodents, S: shrub cover (%), R: rock cover (%), T: tree cover (%). The multiplicative symbol (x) indicates an interaction term.
*K: number of parameters in the model. Loglik: log-likelihood. W: Akaike's weight. R^2_c and R^2_m give conditional and marginal proportion of variance explained. X indicates that the variable was included in the model. Boldface and asterisks indicate statistical significance (*p < 0.05, **p < 0.01, ***p < 0.001). Interactions not included in the best models are not shown for simplicity.*

record of *M. spretus*, and a few visits that could not be identified to species level. Rodents consumed 30.4% of the dispensed seeds (n = 350), with 57% of the predation occurring in lynx presence (Figure 2B). We recorded a total of 109 independent rodent visits to the seed depots via camera trapping, with most of them (85%) occurring in lynx presence (Figure 2A). Rodents consumed seeds in 19% of the visits. The average visit duration was 66.1 ± 13.7 s.

Seed Predation by Rodents

We identified three top-ranked models (ΔAIC < 2) for seed predation rates in the experiment, none of which included lynx presence or its interactions (Table 1). The variables that best explained seed predation rates were microhabitat type and relative abundance of rodents (RAI) (Table 1). The microhabitat with the highest seed predation was the shrub type, compared to the other microhabitats (marginal mean, 95% CI) (shrub: 0.1, 0.05—0.22; rock: 0.03, 0.02—0.08; open: 0.01, 0.01—0.03; P < 0.001) (Figure 2B). RAI had a positive effect on the proportion of seeds predated by rodents (Appendix S1: Table S1). Shrub and tree cover were included in a single model and did not have a significant effect on seed predation rates (Table 1). Although lynx presence did not significantly affect seed predation, the cumulative proportion of seeds predated was lower in the lynx absence scenario throughout the experiment (see Appendix S2: Figure S1).

Activity and Foraging Behavior of Seed-Eating Rodents

Regarding the seed encounter probability during visits, the best model included lynx presence/absence and shrub and tree cover (Table 1). The model-estimated probability of seed consumption was significantly lower in the lynx presence scenario compared to the lynx absence (P = 0.006; Figure 3A). We observed proportionally more visits with no seed consumption in lynx presence sites (83%), particularly from the third day of the experiment (Appendix S2: Figure S2). In lynx absence, the number of visits with and without seed consumption was quite similar (Figure 3B). Shrub cover negatively affected the probability of seed encounter, while tree cover had a positive effect (Appendix S1: Table S1).

For the frequency of visits to seed depots, two top-ranked models were selected, both including the interaction between lynx presence and micro-

habitat type, as well as covariates for RAI and shrub and rock cover (Table 1). The models estimated that the number of visits to seed depots located under shrubs was significantly higher in lynx absence areas compared to lynx presence (marginal mean, 95% CI) (2.7, 1.3—5.6 vs. 0.4, 0.2—1.1; P = 0.004). RAI had a positive effect on the number of rodent visits, as did rock cover (Table 1, Appendix S1: Table S1). Conversely, shrub cover had a negative effect on the number of visits in overall (Table 1, Appendix S1: Table S1). Only one of the two top models included the interaction between lynx presence and habitat type (Table 1), but no significant differences were found in the number of visits between lynx presence and absence across different habitats. However, the number of rodent visits to seed depots was significantly higher in forest habitats compared to open habitats, regardless of lynx presence (4.6, 1.5—14.7 vs. 0.1, 0.03—0.7; P = 0.005).

Fourteen top-ranked models were selected for the visit duration at seed depots, which included interactions between lynx presence/absence and seed encounter probability, lynx presence/absence and habitat and microhabitat type, as well as the interaction between habitat and microhabitat type. Some of these models also included the RAI, and the cover of shrubs, trees, and rocks (Appendix S1: Table S2). Lynx presence had a positive and significant effect on the visit duration in forest habitats (P = 0.01; Figure 4), while no significant differences were found between microhabitats (Appendix S1: Table S1). Seed consumption during visits had a positive and significant effect on the duration of the visits (P = 0.01; Appendix S1: Table S1). Rock cover had a significant and positive effect on the visit duration (P = 0.04; Appendix S1: Table S1), but the relative abundance of rodents (RAI), shrub, and tree cover did not have a significant effect on the visit duration (Appendix S1: Table S1).

Discussion

Our study reveals a behaviorally mediated trophic cascade triggered by an apex predator, the Iberian lynx, which influences the foraging behavior of seed-eating rodents that are also prey for mesopredators. Contrary to expectations, we did not detect higher rodent abundance or seed predation rates in lynx-occupied areas (see Burgos and others 2025). This discrepancy may reflect limitations in our sampling design and temporal window, in contrast with the broader spatial and temporal scope of previous studies in the same system, such as Burgos and others (2023). Nevertheless, we found that rodents altered their foraging behavior in response to lynx presence, making more frequent visits without seed predation, spending more time in forest habitats, and showing a lower probability of seed consumption. By altering post-dispersal seed predation patterns, these behavioral changes may ultimately reduce the seed dispersal effectiveness (Schupp and others 2010) and hinder the recruitment success of plants such as *Pyrus bourgaeana* in rewilding scenarios involving apex predators.

Apex Predators as Top-Down Regulators

The top-down control exerted by apex predators on prey has been extensively studied (Estes 1996; Ripple and Beschta 2007, 2012). However, apex predators can also indirectly influence the abundance and behavior of small prey species by regulating their primary predators (Letnic and others 2012; Miller and others 2012). In southern Spain, the Iberian lynx is the largest terrestrial predator and has come back as a novel predator in the trophic web in areas where it has been reintroduced or recovered. Several studies have documented a significant reduction in the abundance and occupancy of mesopredator communities in regions inhabited by lynx or where lynx have been recently reintroduced (Jiménez and others 2019; Burgos and others 2023). Consequently, common and widely distributed mesopredators, such as the red fox, stone marten, or common genet (Genetta genetta), which frequently prey on small species like rodents (Monterroso and others 2020), have experienced local population declines. Small mammals play a dual role in trophic webs, serving as prey for carnivores and as both seed dispersers and seed predators for many plant species (Rey and others 2002; Fedriani and others 2020). Therefore, an apex predator like the Iberian lynx can trigger cascading effects on ecosystem functions such as seed dispersal or seed predation, ultimately influencing plant establishment and regeneration processes (de Paula and others 2018; Burgos and others 2024; Fedriani and others 2024).

Reduced predation pressure due to the presence of apex predators can lead to an increase in the abundance of small mammal species, such as rodents (Miller and others 2012; Gordon and others 2015). In the specific case of the Iberian lynx, Burgos and others (2023) found that this prey release effect is particularly significant for large rodent species, such as the garden dormouse, which can provide a high-energetic reward for

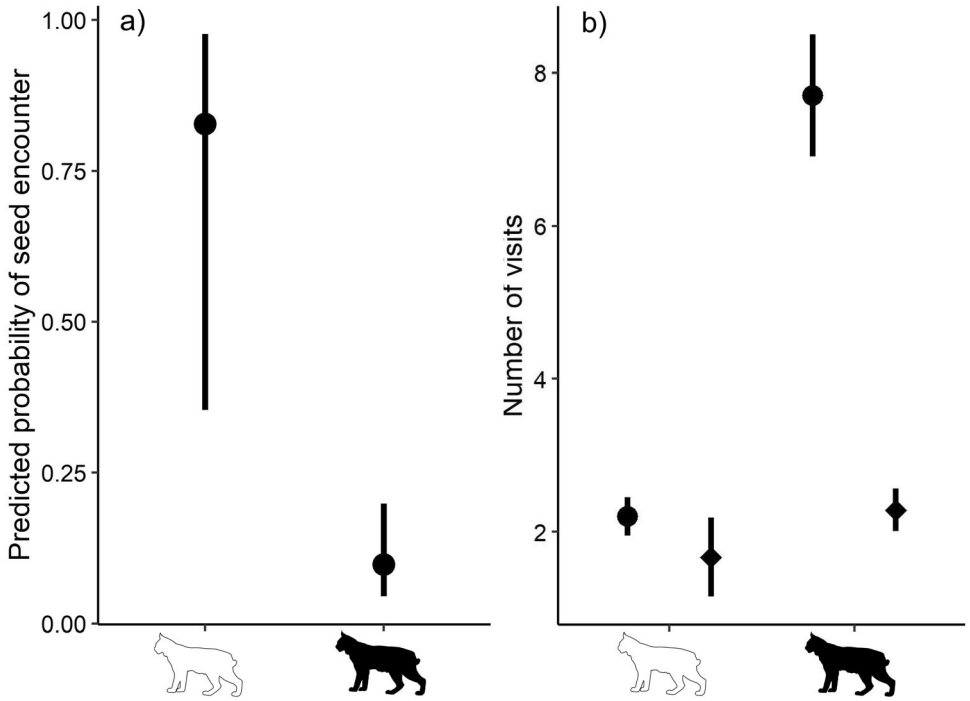


Figure 3. (a) Mean predicted values of seed encounter probability model. Error bars represent the 95% confidence intervals from model predictions. (b) Mean number of visits without and with seed consumption represented by circles and diamonds, respectively. Error bars show the standard errors of observations. Lynx absence is represented by white-lynx silhouette and lynx presence by black-lynx silhouette.

mesopredators (Santos and others 2020). However, we did not observe a lynx' effect on the local abundance of rodents, likely because our study focused on the post-dispersal stage of *P. bourgaeana*, and rodent abundance was only surveyed during this period (autumn–winter). The garden dormouse is inactive in winter due to adverse weather conditions, despite inter-individual variation in hibernation patterns exists (Moreno 1988). This explains why only one juvenile garden dormouse was captured in our live traps, with the remainder being wood mice. Therefore, the absence of a cascading effect on seed predation rates by rodents may be attributed to the dominance of the wood mouse in our study area during winter, which appears to be the species least affected by this tri-trophic cascade (Burgos and others 2023). The lack of significant lynx effect on rodent abundance could also be partially explained by our relatively small trapping effort, which could have limited our power to detect significant abundance differences. Nevertheless, shrubs are the preferred microhabitat for rodent foraging, as they reduce the likelihood of predator detection (Rey and others 2002; Loggins and others 2019). Because shrub availability was greater in lynx-free areas than in lynx territories, such higher shelter availably for rodents could have compensated for the increased predation risk in these areas, thereby mitigating the strength of the expected cascading effects.

The presence of a cascading effect on visit rates to seed depots, but not on seed predation rates, could be also due to mice consuming more seeds per visit in lynx-unoccupied areas. For instance, Manson and Stiles (1998) found that the spatial patterns of seed removal did not always correlate with the distribution and abundance of mice. It is also possible that the limited number of seeds per depot or a greater preference for other available food sources (Alcántara and others 2000; Suárez-Esteban and others 2018), constrained our ability to detect lynx-related differences in seed predation rates. These findings suggest that the impact of rodent abundance on spatial patterns of seed survival after seed dispersal may be more dependent on the behavioral responses of rodents than on the distribution of the populations they constitute (Boone and others 2022). Thus, rodents may compensate for fewer visits in high-predation-risk scenarios by balancing post-dispersal seed predation rates inside and outside lynx territories. However, it was not possible to quantify the number of seeds consumed per visit using the images captured by our cameras.

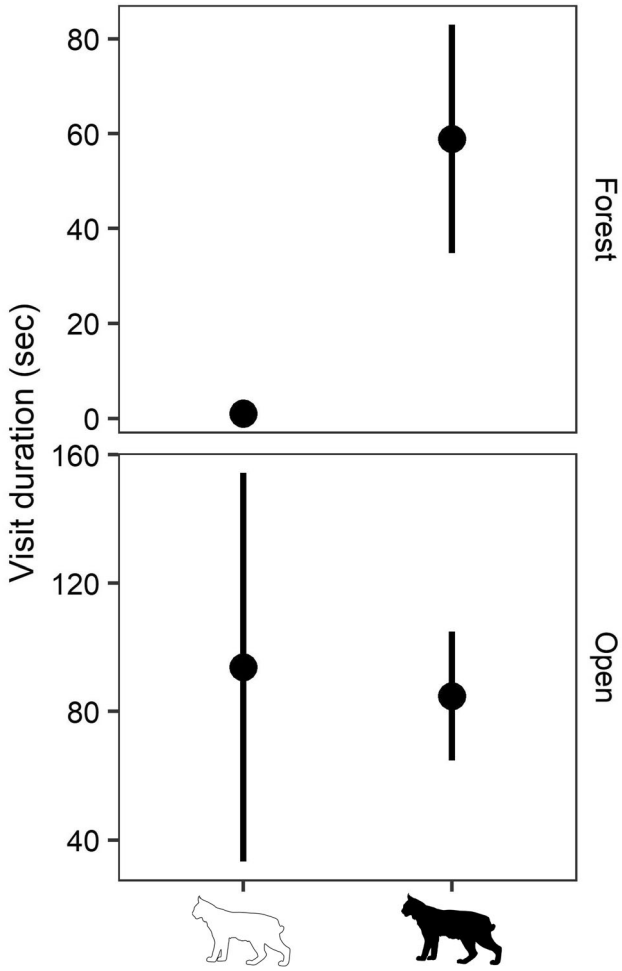


Figure 4. Average time per visit in seconds for lynx absence (white-lynx silhouette) and lynx presence scenario (black-lynx silhouette) in forest and open habitats. Bars indicate standard errors.

On the other hand, we observed higher seed predation and visit rates at seed depots in areas with higher rodent abundance, consistent with previous studies (Schnurr and others 2004; Pender and others 2013). This indicates that rodent abundance could also have a significant effect on post-dispersal seed predation rates, and thus, higher rodent abundance could also contribute to limit the availability of viable seeds for plant recruitment locally (Vaz Ferreira and others 2011; Galetti and others 2015b; Garrote and others 2019). Therefore, further research is warranted to explore how seasonal changes in rodent communities and their abundance can influence seed predation rates across different predation risk scenarios, such as the one presented in this study.

Cascading Effects on the Foraging Behavior and Activity of Rodents

Trophic cascades can also occur through non-lethal interactions via behavioral changes in response to perceived predation risk, referred to as behaviorally mediated trophic cascades (Schmitz and others 1997, 2004). Apex predators create a landscape of fear that not only alters the abundance but also the foraging behavior and activity of subordinate species, and consequently, their prey (Laundré and others 2010; Gaynor and others 2019). Our results corroborate a shift in foraging behavior of rodents between sites with and without lynxes. It appears that the presence of this apex predator leads rodents to take greater risks and engage in longer exploratory feeding visits, likely due to a perceived reduction in predation risk because of the lower abundance of mesopredators (Burgos and others 2023). This occurs primarily in habitats that provide refuge, such as forests (Kotler and Brown

1988; Sunyer and others 2013; Boone and others 2022). Overall, these patterns suggest that both numerical and behaviorally mediated trophic cascades may operate simultaneously, shaping post-dispersal seed predation dynamics in this system.

Conversely, rodents that do not coexist with the Iberian lynx, and therefore face greater predation pressure from mesopredators such as martens or genets, seem to make shorter feeding visits in forest habitats. Although these habitats offer more refuge, they may also support a higher abundance and diversity of both terrestrial and avian predators (Pita and others 2009; Moreno-Mateos and others 2011). Additionally, rodents made significantly more visits to shrub microhabitats only at sites without lynx presence. The combination of increased shrub availability and elevated mesopredator activity in lynx-free areas may drive rodents to concentrate their foraging activity in structurally complex microhabitats that enhance concealment and reduce the likelihood of predator detection (Rosalino and others 2011; Loggins and others 2019). Similar results were reported by Brown and others (1988), who found that in response to the presence of barn owls, three species of heteromyid rodents shifted their habitat use toward shrub microhabitats, reduced foraging, and left resource patches at higher giving-up seed densities. However, in areas with lower predation pressure according to our experimental design (that is, in lynx-occupied sites), rodents used all available microhabitats, including open interspaces. Gordon and others (2015) found similar results for desert rodents in Australia, which increased their habitat selection breadth and use of risky foraging patches in areas where dingoes (*Canis dingo*) were present but mesopredators were scarce. It is also possible that in predator-free scenarios with a richer and more abundant small prey community (Jiménez and others 2019; Burgos and others 2023), rodents use all available microhabitats as a mechanism to avoid intra-guild competition.

Although rodents consumed a similar number of seeds at sites with and without lynx, they made more visits to the seed depots in the presence of the apex predator, with most of these visits not involving seed consumption. Consequently, the probability of seed consumption per visit was higher at sites without lynx (high predation risk) compared to sites with lynx (low predation risk), which is likely due to rodents maximizing their exploratory feeding excursions in the high-risk scenario (see Figure 3). However, studies comparing seed removal probability of rodents across scenarios varying in perceived predation risk have failed to identify a generalized pattern, likely due to inter and intra-specific differences (Rey and others 2002; Fedriani and Manzaneda 2005; Boone and others 2022; Morán-López and others 2022). Moreover, there is still a gap of knowledge evaluating how the probability of fruit or seed consumption by subordinate species in the food chain can be altered as a consequence of trophic cascades initiated by an apex predator (but see Ripple and others 2014b; Carreira and others 2020; Burgos and others 2022, 2024).

The negative effect of tree and shrub cover surrounding our experimental plots on rodent activity patterns (for example, visit rates, seed consumption probability) could be explained by a greater availability of preferred food resources in areas with denser vegetation. In such contexts, rodents may shift their foraging efforts toward these alternative, more attractive food resources (for example, Fedriani and Manzaneda 2005). Specifically, the availability of oak acorns (*Quercus ilex, Q. coccifera, Q. suber*) could be a key factor determining rodent habitat use in Mediterranean ecosystems (Diaz and Alonso 2003; Torre 2004). Conversely, the positive effect of rock cover on both the number and duration of visits may reflect the added structural complexity of this microhabitat, which likely reduces perceived predation risk and provides rodents with a greater sense of safety (Mandelik and others 2003). This interpretation aligns with our finding that rodents made longer visits to rocky microhabitats only in open areas, where exposure to predators would otherwise be higher.

Future Challenges for Behaviorally Mediated Trophic Cascades

The anti-predatory behaviors revealed in our study have the potential to significantly impact food webs and ecosystem functioning. Habitat-mediated preferences can influence plant recruitment and seedling establishment (Schupp 1995; García and others 2005; Vaz Ferreira and others 2011; Burgos and others 2025), especially when behaviorally mediated trophic cascades lead to differential habitat use by seed predators. For example, the preference for shrub microhabitats observed under lynx presence may intensify seed predation in microsites that are typically more favorable for seedling establishment, thereby limiting the probability of a seed to develop into an adult plant (Bartel and Orrock 2021; Burgos and others 2025). The presence of apex predators like the Iberian lynx could also have positive effects on ecosystem functioning

and indirectly benefit other species (Sergio and others 2008; Ripple and others 2014a). Nevertheless, the ecological consequences of restoring apex predators for plants in altered ecosystems remain largely unknown (but see Maron and Pearson 2011; Burgos and others 2024), and thus, caution and further research are certainly needed.

On the one hand, apex predators may trigger contrasting cascading effects down to plants, as post-dispersal seed predation by rodents can vary among plant species (Rey and others 2002). The garden dormouse increases its activity in spring and summer after hibernation (Moreno 1988). In addition, this species shows a marked release from predation in areas with Iberian lynx, leading to higher local abundances (Burgos and others 2023). Together, these factors could limit the number of available post-dispersal seeds from Mediterranean plants fruiting during summer, such as blackberry (*Rubus sp.*) and Mediterranean Buckthorn (*Rhamnus alaternus*), particularly in lynx areas. Likewise, we found that in lynx-occupied areas, rodents spent more time foraging in forest habitats—presumably due to lower predation risk—which could increase seed predation pressure on forest-dwelling plant species that are more attractive or accessible in these environments, potentially limiting their recruitment. On the other hand, a greater abundance of scatter-hoarding rodents in scenarios of apex predator rewilding could also positively impact plant recruitment by facilitating the secondary dispersal of acorns (*Quercus* sp.) and other large-seeded species (Gómez and others 2008; Cao and others 2011). Moreover, rodents may also act as seed rescuers by extracting viable seeds trapped within aborted fruits, thus enhancing opportunities for seedling establishment (Fedriani and others 2020).

It would be valuable to consider other potential factors influencing rodent seed predation and foraging behavior in future research, such as nocturnal raptor abundance, seasonality or finer-scale habitat complexity. Furthermore, it would be worthwhile to investigate the interactions among species across different trophic levels within this food web under a ''before–after'' experimental design, especially now that we have the opportunity to assess these ecological questions in planned lynx reintroduction areas. Although our design did not include spatial replication at the lynx presence/absence level, this was based on prior evidence from the same study system demonstrating strong and consistent top-down effects of lynx on mesopredator and rodent communities through large-scale camera-trap monitoring (Burgos and others 2023). Future studies could complement this approach with broader spatial and temporal replication to better capture context-dependent and species-specific dynamics. Apex predator rewilding could offer one of the best, yet rare, opportunities to evaluate how the ecological context may influence the strength of predator effects on the structure and function of ecosystems.

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DATA AVAILABILITY

Data are publicly available in the Environmental Data Initiative (EDI) repository at https://doi.org/10.6073/pasta/1845b6ac44c9596cffe29ce6af7749dc.

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